

Reproductive biology of *Carcharhinus acronotus* in the coastal waters of South Carolina

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(Received 25 June 2003, Accepted 26 February 2004)

The reproductive biology of blacknose sharks *Carcharhinus acronotus* in the western North Atlantic Ocean was studied by examining specimens collected in the coastal waters of South Carolina. Males begin the maturation process between 875 and 910 mm fork length (L_F), as indicated by the presence of functional claspers and siphon sacs. The presence of vitellogenic oocytes and developing oviducal glands and uteri indicated that females begin to mature at *c.* 870 mm L_F . Length at which 50% of the population reached maturity was 896 and 964 mm L_F , equivalent to 4.3 and 4.5 years, for males and females, respectively. Gonado-somatic indices suggested that spermatogenesis and vitellogenesis began after December. Mating took place during the end of May and the beginning of June. Fertilization occurred during late June and early July, suggesting that female blacknose sharks were capable of sperm storage. Based on the timing of fertilization and occurrence of females carrying near-term pups in late May and early June, the gestation period for blacknose sharks was *c.* 11 months. Female blacknose sharks reproduced biennially based on the absence of vitellogenic oocytes in near-term females and there being no indication of vitellogenesis in postpartum females. Male blacknose sharks were capable of reproducing annually as indicated by turgid genital ducts, which were observed in all mature males collected during late May and early June.

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Key words: Carcharhinidae; gestation period; small coastal shark; spermatogenesis; vitellogenesis.

INTRODUCTION

The distribution of the blacknose shark *Carcharhinus acronotus* (Poey) is limited to the western Atlantic Ocean with its range extending from North Carolina to Brazil, including the Gulf of Mexico (Castro, 1983; Compagno, 1984). Blacknose

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sharks frequently constitute a substantial portion of the catch in coastal fisheries throughout their range and are often targeted due to their economic value (Trent *et al.*, 1997; Cortés, 2002). In coastal waters of the south-eastern United States, the National Marine Fisheries Service manages blacknose sharks in the small coastal shark complex, a group which also includes the finetooth shark *Carcharhinus isodon* (Müller & Henle), Atlantic sharpnose shark *Rhizoprionodon terraenovae* (Richardson) and bonnethead shark *Sphyrna tiburo* (L.) (NMFS, 1993).

Several studies have examined general aspects of the reproductive biology of blacknose sharks. Depending on area, the size at maturity for blacknose sharks has been estimated to be between 970 and 1100 mm total length (L_T) for males and 1012 and 1187 L_T for females (Clark & von Schmidt, 1965; Dodrill, 1977; Schwartz, 1984; J.K. Carlson, unpubl. data). In terms of age at maturity, Clark & von Schmidt (1965) stated that both male and female blacknose sharks reach maturity in 2 years while Carlson *et al.* (1999) estimated that female blacknose sharks mature in 3.0 years and males in 2.5 years in the Gulf of Mexico. There is also disagreement regarding the reproductive cycle and gestation period of blacknose sharks. In the western North Atlantic Ocean, Dodrill (1977) determined that female blacknose sharks reproduce biennially and suggested a gestation period of 10–11 months, while Schwartz (1984) concluded that reproduction occurs annually with gestation lasting 9 months. Moreover, in the western South Atlantic Ocean off Brazil, Hazin *et al.* (2002) was unable to resolve the reproductive cycle but hypothesized that gestation lasts for *c.* 8 months and females reproduce annually. Given the uncertainties associated with the reproduction of this species, the objectives of the present study were to provide a quantitative study of the reproductive biology for blacknose sharks in coastal waters off the south-eastern U.S.A.

MATERIALS AND METHODS

A total of 241 blacknose sharks (113 males and 128 females) were collected from coastal waters off South Carolina, U.S.A. from July 1998 to June 2001. Blacknose sharks were collected using bottom longline and handline fishing gear. The bottom longline gear consisted of 1829 m of mainline (272 kg test monofilament) with 120 gangions. The handline gear consisted of 180 m braided rope mainline, with an 18.3 m anchor depth, and supported the use of 50 gangions at 2.8 m intervals. The gangions for both gear types were 63 cm in length and had 91 kg test monofilament leaders and 15/0 tuna circle hooks. The gear was baited with various species of teleosts (as determined by seasonal availability) and set at depths ranging from 2 to 14 m. Soak times were limited to 1 h to reduce mortality rates in non-target species. After collection, sex was recorded and fork length (L_F) was measured to the nearest mm over a straight line along the axis of the body. Stretch L_T was measured from the anterior tip of the snout to the posterior tip of the upper lobe of the caudal fin while fully extended (Castro, 1993a). The mass of each shark was measured to the nearest 0.5 kg when sampling conditions permitted. All sampling effort occurred within 5.5 km of the South Carolina coast (Fig. 1).

MALES

The length of the right clasper (mixopterygia) was measured and state of maturity recorded. Maturity was determined by the presence of calcified claspers that rotated 180° relative to their normal position, a freely opening rhipidion and fully developed siphon

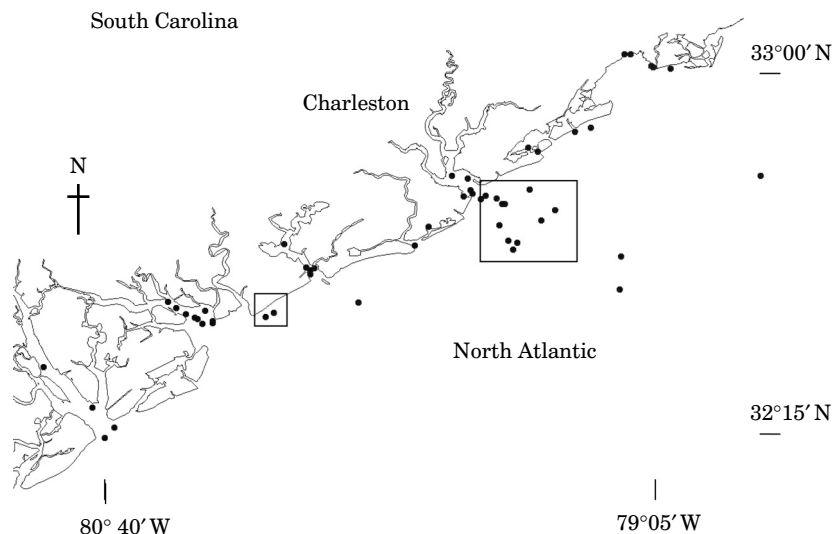


FIG. 1. Sampling locations within South Carolina waters. □, areas where the majority of blacknose sharks were collected.

sacs (Clarke & von Schmidt, 1965). The presence of sperm was not considered to be an indication of maturity because sperm production can occur before the claspers are adequately calcified to facilitate copulation (Pratt, 1996). The claspers were measured from the cloacal apex to the posterior free tip. The siphon sacs of mature males were measured by placing the tip of an irrigation bottle through the apophyle and applying pressure. Once inflated, the right siphon sac was measured from the cloacal apex to the distal point of inflation. The right testis was excised from the epigonal organ and the length, width and mass of the testis were measured. The condition of the epididymides and the ductus deferens was noted, and the genital ducts were inspected for the presence of seminal fluid. To correct for unequal samples sizes, a non-paired *t*-test (Zar, 1974) was used to compare testes dimensions between mature and immature males and between mature males with regressed and turgid testes.

FEMALES

The widths of the right oviducal gland and right uterus (only in non-gravid females) were measured. The right ovary was excised and stored in a plastic bag on ice and then frozen. After thawing, all epigonal tissue was removed and the ovary was weighed and all exposed ova were measured. The stage of oocyte development was classified as undeveloped, developing, yolked or atretic. Females were considered mature if they were gravid or had developing ova, enlarged oviducal glands and developed uteri (Castro, 1993a). ANOVA and non-paired *t*-tests (Zar, 1974) were used to test for monthly differences in mean oocyte diameter. ANOVA was used to determine if there were significant differences in oviducal gland width by month. The uteri, if developed, were dissected to determine if embryos or uterine eggs were present. If embryos were present their mass, L_F and sex were recorded. The relationship between maternal L_F and litter size was compared using ANOVA and linear and non-linear regression.

ESTIMATION OF SIZE AND AGE AT MATURITY

To determine size and age at which 50% of the population was mature, a logistic model, $Y = (1 + e^{-(a+bx)})^{-1}$, was fitted to binomial maturity data using least squares non-linear regression. Median L_F and age at maturity were determined as $-a/b^{-1}$ (Mollet *et al.*, 2000). Direct age estimates were made using vertebral centra as described by Driggers *et al.* (2004).

REPRODUCTIVE CONDITION

Gonado-somatic indices (I_G) were calculated to estimate the time of vitellogenesis, ovulation and spermatogenesis. The I_G for each shark was calculated using the following modified equation (Nikolsky, 1963): $I_G = 100[\text{gonad mass} (\text{mass of animal} - \text{gonad mass})^{-1}]$. I_G values for mature males from late May and early June were pooled for all calculations. Because not all sharks were weighed due to sampling constraints, in some instances ($n = 15$ males and two females) body mass was determined, using the regressions; body mass = $e^{(-1.892 + 0.004 L_F)}$ (ANOVA, $n = 120$, $P < 0.01$, $r^2 = 0.96$) for females and body mass = $e^{(-1.673 + 0.004 L_F)}$ (ANOVA, $n = 102$, $P < 0.01$, $r^2 = 0.95$) for males. ANOVA and Scheffe's multiple range test (Zar, 1974) were used to examine differences in mean I_G values by month.

RESULTS

MALES

Sixty-seven immature and 46 mature blacknose sharks were examined over the course of this study. The size at 50% maturity for male blacknose sharks was 896 mm L_F ($a = -116.46$, $b = 0.13$, $r^2 = 0.92$) at an age of 4.3 years ($a = -13.42$, $b = 3.15$, $r^2 = 0.93$). The smallest mature male blacknose shark was 875 mm L_F and the largest immature male was 926 mm L_F . At *c.* 830 mm L_F the claspers of male blacknose sharks rapidly increased in length (Fig. 2). The claspers were fully calcified, able to rotate, and the rhipidion functional between 875 and 910 mm L_F . The length of the claspers was $11.9 \pm 0.7\%$ (all means presented \pm s.d.) of L_F once maturity was reached ($n = 45$). The siphon sacs were functional at *c.* 890 mm L_F (Fig. 3).

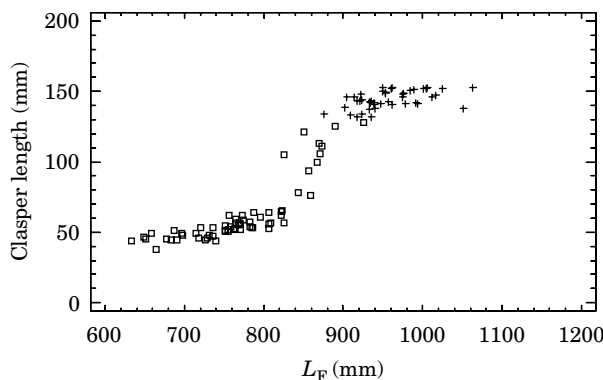


FIG. 2. The relationship between fork length and clasper length of immature (\square) and mature ($+$) male blacknose sharks ($n = 113$).

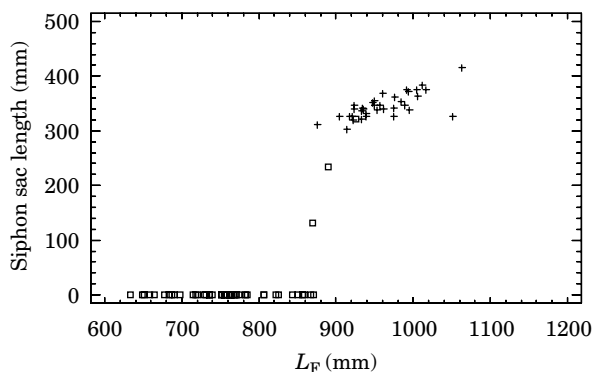


FIG. 3. Relationship between fork length and siphon sac length of immature (\square) and mature (+) male blacknose sharks ($n = 113$).

There was a significant difference between the testes length of immature males and mature males with regressed gonads (t -test, $n = 84$, $P < 0.01$). The testes width of immature males and mature males with regressed testes, however, were not significantly different (t -test, $n = 84$, $P = 0.09$). This indicated that the testes width is not a good criterion for the assessment of maturity. There was a significant difference between the lengths of the testes in mature males whose epididymides and ductus deferii were turgid and non-turgid (t -test, $n = 46$, $P < 0.01$).

ANOVA and multiple range tests for each of the measures indicated that there were no significant differences in I_G values from mid-June to December ($P = 0.53$) thus indicating that spermatogenesis commenced after December and before May of each year. The I_G established that late May to early June was the peak time of sperm production as the testes of male blacknose sharks attained their maximum size during this period (Scheffe's multiple range test) (Fig. 4). The epididymides and ductus deferens of all mature males ($n = 19$), caught in late May and early June of 1999 and 2000, contained copious amounts of seminal fluid (*c.* 40 ml per genital duct).

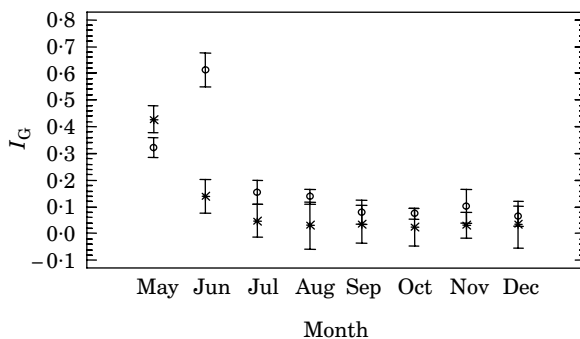


FIG. 4. Mean \pm 95% CI gonado-somatic indices for male (\times) ($n = 46$) and female (\circ) ($n = 20$) blacknose sharks by month (juveniles and gravid females excluded).

FEMALES

A total of 82 immature and 46 mature female blacknose sharks were examined. The size at 50% maturity for female blacknose sharks was 964 mm L_F ($a = -115.70$; $b = 0.12$; $r^2 = 0.78$) at an age of 4.5 years ($a = -35.97$; $b = 8.09$; $r^2 = 0.91$). The largest immature female blacknose shark was 958 mm L_F and the smallest mature female was 910 mm L_F . At *c.* 870 mm L_F , the uteri of immature females began to enlarge (Fig. 5). The mean width of the uteri observed in immature females, prior to the onset of maturation, was 2.47 ± 0.74 mm ($n = 28$). Once maturation was complete, the mean uterus width was 15.51 ± 6.60 mm ($n = 12$) in non-gravid and non-ovulating females.

The mean width of the right oviducal gland in immature female blacknose sharks was 6.44 ± 1.20 mm ($n = 49$). Once the maturation process began the oviducal glands grew rapidly (Fig. 6). ANOVA indicated that there was a significant difference in oviducal gland widths in ovulating and non-ovulating females ($P < 0.01$). The mean oviducal gland width observed from May to December in gravid, postpartum (as indicated by flaccid uteri and placental scars) and non-ovulating adults was 22.76 ± 2.48 mm ($n = 40$). The mean oviducal gland width in ovulating females increased to 35.35 ± 2.99 mm ($n = 4$) in late June to early July. These data indicated that the width of the oviducal glands significantly increased just prior to ovulation and then rapidly regressed after fertilization (*t*-test, d.f. = 42, $P < 0.01$).

Numerous follicles *c.* 1–2 mm in diameter were present in the right ovary of immature females. During the maturation process and non-gravid portion of the reproductive cycle, an average of 9.65 ± 5.68 ovarian follicles began to develop. The mean width of developing oocytes from July to October was 6.24 ± 0.87 mm. The mean oocyte diameter increased to 7.30 ± 0.60 mm in November. Oocyte diameter continued to increase in December to 8.80 ± 1.67 mm. That value was significantly different from the oocyte diameter from late July to October (*t*-test, d.f. = 220, $P < 0.01$), but not significantly different from the mean diameter in November (*t*-test, d.f. = 84, $P = 0.22$). The mean oocyte diameter increased to 21.85 ± 2.62 mm by May and was significantly different than the oocyte diameter in December (*t*-test, d.f. = 68, $P < 0.01$). From May to early July, no significant difference was found in

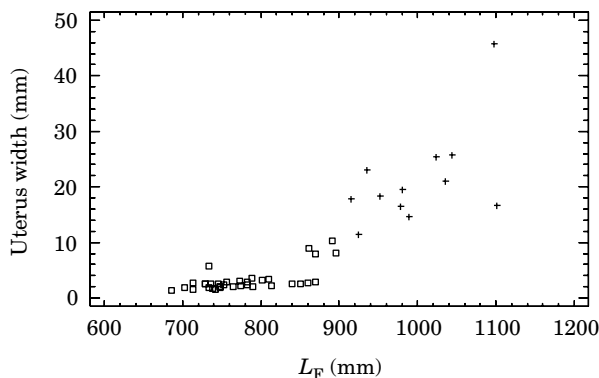


FIG. 5. Relationship between fork length and uterus width of immature (□) and mature (+) female blacknose sharks ($n = 47$) (gravid, postpartum and ovulating females excluded).

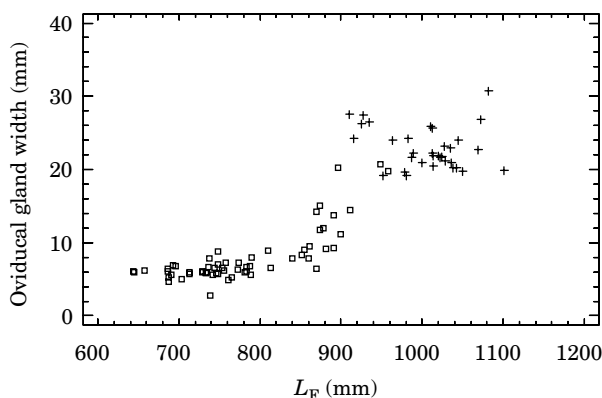


FIG. 6. The relationship between fork length and oviducal gland width of immature (□) and mature (+) female blacknose sharks ($n=93$) (ovulating females excluded).

mean oocyte diameter (ANOVA, $F_{1,31}$, $P=0.06$) and maximum mean oocyte diameter during this period was 28.83 ± 3.09 mm. Mean diameter of ovarian follicles in the right ovary of two gravid females with near-term pups caught in late May and early June of 2001 was 7.59 ± 1.34 mm. Additionally, postpartum females ($n=7$) showed no sign of vitellogenesis.

A significant linear relationship was found between maximum follicle diameter and ovary mass (ANOVA, $F_{1,39}$, $P<0.01$, $r^2=0.91$). A multiple range test indicated no difference in the mean I_G from July to December (pooled mean = 0.10 ± 0.04). I_G increased in May (mean = 0.32 ± 0.11) and reached a maximum in June (mean = 0.61 ± 0.13). A significant difference in mean monthly I_G value between June and July (ANOVA, $F_{1,2}$, $P<0.01$) was found indicating female blacknose sharks ovulate in late June (Fig. 4). This is also supported by the presence of uterine eggs and regressed oviducal glands observed in all gravid females captured in mid to late July.

UTERINE DEVELOPMENT

Among pregnant females ($n=26$), pups in varying stages of development were identified. After the blastodisc stage of development, all embryos were encased in egg envelopes within individual uterine compartments. By late September, the yolk sac and stalk had differentiated into the placenta and umbilical cord. The mean number of pups carried by each female was 3.53 ± 0.70 . The maximum number of pups was five and the minimum one. Uterine growth was initially slow. By the end of the second month of gestation uterine growth became more rapid (Fig. 7). There were insufficient data, however, to generate a growth curve for uterine development because no blacknose sharks were collected from late December to May. A significant linear relationship was found between maternal length and the number of pups per litter (ANOVA, $F_{1,17}$, $P=0.02$, $r^2=0.26$). The ratio of male to female embryos was 1:1.11, which was not significantly different from 1:1 (χ^2 with Yates' correction, d.f. = 1, $P=0.92$).

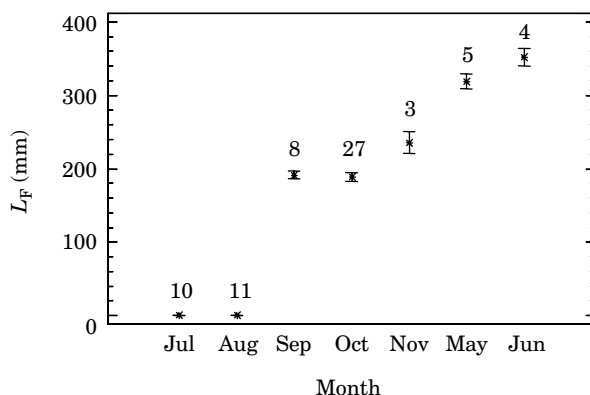


FIG. 7. Mean \pm 95% CI fork length of blacknose shark embryos by month. Numbers above error bars indicate number of embryos collected per month. No blacknose shark embryo samples were collected from December to April.

DISCUSSION

Past studies on the reproductive biology of blacknose sharks have presented little information regarding males (Schwartz, 1984; Hazin *et al.*, 2002). Based on the data from the present study, mature male blacknose sharks in the western North Atlantic initiate spermatogenesis some time after December, as all mature males caught between mid-June and December had regressed testes. During late spring, all mature males captured had turgid testes and well developed genital ducts. This condition persisted until mid-June, indicating that adult male blacknose sharks are capable of reproducing annually for a limited period from late May to early June. Testes rapidly regressed after mating and were visibly indistinguishable from the testes of immature males, a condition also reported for finetooth sharks (Castro, 1993a).

The reproductive cycle for female blacknose sharks is typical of other carcharhinids off the south-eastern U.S.A. such as the finetooth shark (Castro, 1993a). Vitellogenesis begins in mature females during November prior to migrating to their wintering grounds. During late May and June, non-gravid females have large (*c.* 30 mm in diameter) yolked eggs loosely attached to the ovary, which are similar in size to oocytes from ovulating females reported by Hazin *et al.* (2002). During late June and early July, females have enlarged oviducal glands and uterine eggs. By mid-July all gravid females have regressed oviducal glands, atretic ovarian follicles and uterine eggs, therefore, ovulation occurs from late June to early July.

Although not specifically investigated in this study, evidence of a mechanism for sperm storage in female blacknose sharks exists. Females ovulate and ova are fertilized in late June to early July. Males are reproductively active, however, only during the beginning of June, as indicated by the presence of seminal fluid in male genital tracts and females bearing fresh mating wounds (W.B. Driggers, pers. obs.). These observations suggest that female blacknose sharks store sperm for at least a 2 week period prior to ovulation. This is

consistent with Pratt (1993) who demonstrated that other carcharhinids are capable of storing sperm from weeks to months in the oviducal glands.

Positive correlations have been shown between maternal L_F and litter size in spiny dogfish *Squalus acanthias* L. (Jones & Ugland, 2001), spotted gully sharks *Triakis megalopterus* (Smith) (Smale & Goosen, 1999), smoothhound sharks *Mustelus canis* (Mitchell) (Conrath & Musick, 2002) and Atlantic sharpnose sharks (Carlson & Baremore, 2002; Loefer & Sedberry, 2003; G. Parsons, unpubl. data). A significant but weak relationship between litter size and maternal L_F was also found in this study for blacknose sharks. Due to the low mean litter size for blacknose sharks and the small sample size in this study, however, additional litters need to be examined before it can be conclusively stated that fecundity increases with maternal size.

Embryonic development is initially very slow. By the second month of gestation, however, growth increased dramatically. Rapid early embryonic growth has been documented in other elasmobranchs such as the sand tiger shark *Carcharias taurus* Rafinesque (Gilmore & Linely, 1983), Pacific angel shark *Squatina californica* Ayres (Natanson & Cailliet, 1986), spotted gully shark (Smale & Goosen, 1999), and Atlantic sharpnose shark (Parsons, 1983). Unfortunately, no females carrying young between the blastodisc stage and 150 mm L_F were caught during this study; therefore, growth could not be measured directly. Placental implantation occurred during the second month of gestation, and the switch from lecithotrophic to matrotrophic mode of feeding probably facilitated the rapid growth of embryos.

The present data suggests that blacknose sharks are born in late May to early June off South Carolina, with a gestation period of *c.* 11 months. The 11 month gestation period is similar to the 10–11 month gestation period reported by Dodrill (1977) but different than the gestation periods of 8 months reported by Hazin *et al.* (2002) and 9 months reported by Schwartz (1984). Although regional differences in gestation are possible among conspecifics it is unlikely that differences exist in blacknose sharks and are probably more a reflection of the interpretation of the data.

The size at birth for blacknose sharks appears to be between 310 and 360 mm L_F . Although only two near-term females were collected over the course of the study, the sharks carried young between 310 and 358 mm L_F . The size of the pups was similar to a 360 mm L_F free-swimming neonate with umbilical remains that was reported from Morehead City, North Carolina (C. Jensen, pers. comm.). In addition, neonates were caught between 383 and 412 mm L_F in early July in the same area off the North Carolina coast (C. Jensen, unpubl. data), and one neonate was caught in South Carolina waters in late July (398 mm L_F) (Castro, 1993*b*).

Castro (1993*b*) suggested that the coastal waters of South Carolina are a nursery ground for blacknose sharks. No neonate blacknose sharks were collected during this study, despite extensive sampling effort with multiple gear types (longlines, handlines, gillnets and trawls) in the estuaries (Bulls Bay, Charleston Harbor, North Edisto, North Inlet, St Helena Sound and Winyah Bay) and near shore waters (Georgetown, Little River, Charleston and Edisto) of South Carolina from 1995 to 2003 (G. Ulrich, unpubl. data) (Fig. 1). It is unlikely that gear selectivity was responsible for the absence of

blacknose shark neonates throughout the sampling because neonates of several different species of carcharhinids were readily captured, including Atlantic sharpnose sharks, which are smaller than blacknose shark neonates. Other species with neonates slightly larger than blacknose shark neonates were also frequently captured, including the finetooth shark, sandbar shark *Carcharhinus plumbeus* (Nardo), blacktip shark *Carcharhinus limbatus* (Müller & Henle), and scalloped hammerhead shark *Sphyrna lewini* (Griffith & Smith). If primary nursery grounds for blacknose sharks exist in the coastal waters of South Carolina, these areas are less well defined than previously observed and apparently do not include estuarine waters that are important to neonates and juveniles of other species of carcharhinid sharks.

Dodrill (1977) stated that female blacknose sharks reproduce biennially. Schwartz (1984) and Hazin *et al.* (2002), however, suggested that female blacknose sharks have an annual reproductive cycle. All mature females caught in this study during late May and early June were either carrying large oocytes or were pregnant, or postpartum. Gravid and post partum females showed no sign of vitellogenesis, thus indicating that female blacknose sharks reproduce biennially. Furthermore, the presence of developing oocytes in the ovaries of non-gravid females in November and December and the absence of vitellogenic ova in gravid females during this period further support a biennial reproductive cycle.

Fifty per cent of the population of blacknose sharks off the South Carolina coast reach maturity at 896 and 964 mm L_F at an age of 4.3 and 4.5 years, for males and females respectively. In the Gulf of Mexico, the length and age at which 50% of the population reached maturity for male and female blacknose sharks were estimated to be 808 and 814 mm L_F at an age of 3.4 and 3.2 years respectively (T.K. Carlson, unpubl. data). Other studies have demonstrated similar differences in reproductive life-history characteristics of other species of sharks between and among regions. For example, Mollet *et al.* (2000) reported that female mako sharks *Isurus oxyrinchus* Rafinesque mature at a larger size in the western North Atlantic Ocean than in southern hemisphere waters. Parsons (1993) found that male and female bonnethead sharks in Tampa Bay mature at a larger size than bonnethead sharks in Florida Bay. Furthermore, Parsons (1993) determined that female bonnethead sharks in Tampa Bay mature at a younger age than females in Florida Bay. Because reproductive differences have been reported in size and age at maturity between and among regions in the present study and others, it will be necessary in the future to investigate the reproductive biology of each species on a regional basis and determine whether these differences are attributable to genetic differentiation or phenotypic plasticity.

The variability in life-history strategies among some shark species in the coastal waters off the south-eastern U.S.A. (Carlson & Parsons, 1997; Carlson *et al.*, 2003; Driggers *et al.*, 2004) stresses the importance of obtaining accurate regionally based life-history data for shark species. Although the reproductive biology of the blacknose shark in the Gulf of Mexico has not been examined future work should investigate the reproductive biology of this species in this region as well as other areas throughout its range. Given the importance of accurate life-history data to the development of population dynamics models

(Cortés, 1999) it will be necessary to examine the life histories of each species that constitutes the south-eastern U.S.A. shark fishery if this resource is to be properly managed.

The authors thank D. Able (Coastal Carolina University), J. Castro, E. Cortés, M. Grace, L. Jones (National Marine Fisheries Service), C. Jensen (North Carolina Marine Resources Division), M. Arendt, J. Loefer, D. Mellichamp, C. Riley, G. Sedberry, B. Stender, P. Tucker (South Carolina Department of Natural Resources), D. Allen, R. Lehnert, J. Quattro, M. Reichert (University of South Carolina) and R. Stringer who all provided assistance in varying capacities. We would also like to thank the anonymous reviewers whose suggestions and comments improved this paper. This is contribution number 1379 of the Belle W. Baruch Institute for Marine and Coastal Sciences.

References

- Carlson, J. K. & Baremore, I. E. (2002). Changes in biological parameters of the Atlantic sharpnose shark: evidence of density dependent regulation? *Marine and Freshwater Research* **54**, 227–234.
- Carlson, J. K. & Parsons, G. R. (1997). Age and growth of the bonnethead shark, *Sphyrna tiburo*, from northwest Florida, with comments on clinal variation. *Environmental Biology of Fishes* **50**, 331–341.
- Carlson, J. K., Cortés, E. & Johnson, A. G. (1999). Age and growth of the blacknose shark, *Carcharhinus acronotus*, in the Eastern Gulf of Mexico. *Copeia* **1999**, 684–691.
- Carlson, J. K., Cortés, E. & Bethea, D. M. (2003). Life history and population dynamics of the finetooth shark (*Carcharhinus isodon*) in the northeastern Gulf of Mexico. *Fishery Bulletin U.S.* **101**, 281–292.
- Castro, J. I. (1983). *The Sharks of North American Waters*. College Station, TX: Texas A&M University Press.
- Castro, J. I. (1993a). The biology of the finetooth shark, *Carcharhinus isodon*. *Environmental Biology of Fishes* **36**, 219–232.
- Castro, J. I. (1993b). The shark nursery of Bulls Bay, South Carolina, with a review of the shark nurseries of the southeastern coast of the United States. *Environmental Biology of Fishes* **38**, 37–48.
- Clark, E. & von Schmidt, K. (1965). Sharks of the central Gulf coast of Florida. *Bulletin of Marine Science* **15**, 13–83.
- Compagno, L. J. V. (1984). Sharks of the world. An annotated and illustrated catalogue of shark species known to date. Part 2: Carcharhiniformes. *FAO Fisheries Synopsis* **125**, 251–655.
- Conrath, C. L. & Musick, J. A. (2002). Reproductive biology of the smooth dogfish, *Mustelus canis*, in the northwest Atlantic Ocean. *Environmental Biology of Fishes* **64**, 367–377.
- Cortés, E. (1999). A stochastic stage-based population model of the sandbar shark in the Western North Atlantic. *American Fisheries Society Symposium* **23**, 115–136.
- Cortés, E. (2002). Stock assessment of small coastal sharks in the US Atlantic and Gulf of Mexico. *Sustainable Fisheries Division Contribution SFD-01/02-152*. Panama City, FL: NOAA/National Marine Fisheries Service, Southeast Fisheries Science Center.
- Dodrill, J. W. (1977). A hook and line survey of the sharks found within five hundred meters of shore along Melbourne Beach, Brevard County, Florida. MS Thesis, Florida Institute of Technology.
- Driggers, W. B. III, Carlson, J. K., Oakley, D., Ulrich, G., Cullum, B. & Dean, J. M. (2004). Age and growth of the blacknose shark, *Carcharhinus acronotus*, in the western North Atlantic Ocean with comments on regional variation in growth rates. *Environment Biology of Fishes* (in press).
- Gilmore, R. G. & Linley, P. A. (1983). Reproduction and embryonic development of the sand tiger shark, *Odontaspis taurus* (Rafinesque). *Fishery Bulletin U.S.* **81**, 201–225.

- Hazin, F. H. V., Oliveira, P. G. & Broadhurst, M. K. (2002). Reproduction of blacknose shark (*Carcharhinus acronotus*) in the coastal waters off northeastern Brazil. *Fishery Bulletin U.S.* **100**, 143–148.
- Jones, T. S. & Ugland, K. I. (2001). Reproduction of female spiny dogfish, *Squalus acanthias*, in the Oslofjord. *Fishery Bulletin U.S.* **99**, 685–690.
- Loefer, J. K. & Sedberry, G. R. (2003). Life history of the Atlantic sharpnose shark (*Rhizoprionodon terraenovae*) (Richardson, 1836) off the southeastern United States. *Fishery Bulletin U.S.* **101**, 75–88.
- Mollet, H. F., Cliff, G., Pratt, H. L., Jr. & Stevens, J. D. (2000). Reproductive biology of the female shortfin mako, *Isurus oxyrinchus* Rafinesque, 1810, with comments on the embryonic development of lamnoids. *Fishery Bulletin U.S.* **98**, 299–318.
- Natanson, L. J. & Cailliet, G. M. (1986). Reproduction and development of the Pacific angel shark, *Squatina californica*, off Santa Barbara, California. *Copeia* **1986**, 987–994.
- Nikolsky, G. V. (1963). *The Ecology of Fishes*. New York: Academic Press.
- NMFS (1993). *Fishery Management Plan for Sharks of the Atlantic Ocean*. Washington, D.C.: U.S. Department of Commerce and Silver Springs, MD: National Oceanic and Atmospheric Administration.
- Parsons, G. R. (1983). The reproductive biology of the Atlantic sharpnose shark, *Rhizoprionodon terraenovae* (Richardson). *Fishery Bulletin U.S.* **81**, 61–73.
- Parsons, G. R. (1993). Geographic variation in reproduction between two populations of the bonnethead shark, *Sphyrna tiburo*. *Environmental Biology of Fishes* **38**, 25–35.
- Pratt, H. L., Jr. (1993). The storage of spermatozoa in the oviducal of western North Atlantic sharks. *Environmental Biology of Fishes* **38**, 139–149.
- Pratt, H. L., Jr. (1996). Reproduction in the male white shark. In *Great White Sharks: The Biology of Carcharodon carcharias* (Klimley, A. P. & Ainley, D. G., eds), pp. 131–138. San Diego, CA: Academic Press.
- Schwartz, F. J. (1984). Occurrence, abundance, and biology of the blacknose shark, *Carcharhinus acronotus*, in North Carolina. *Northeast Gulf Science* **7**, 29–47.
- Smale, M. J. & Goosen, A. J. J. (1999). Reproduction and feeding of spotted gully shark, *Triakis megalopterus*, off the Eastern Cape, South Africa. *Fishery Bulletin U.S.* **97**, 987–998.
- Trent, L., Parshley, D. E. & Carlson, J. K. (1997). Catch and bycatch in the shark drift gillnet fishery off Georgia and East Florida. *Marine Fisheries Review* **59**, 19–28.
- Zar, J. H. (1974). *Biostatistical Analysis*. Englewood Cliffs, NJ: Prentice-Hall Inc.